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Vulnerability of phenological progressions over season and elevation to climate change: *Rhododendrons* of Mt. Yulong

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ABSTRACT

Seasonal timing (phenology) of reproduction is a critical dimension of life-history, affecting ecological and evolutionary processes including individual fitness, community interactions, species boundaries and climate change adaptation. Staggered phenological sequences, or progressions, of flowering in plants have long been a topic of interest. Less well studied are multi-dimensional progressions across seasonal time and elevational space, which may be especially vital to understanding montane and alpine environments that are among the ecosystems most vulnerable to climate change.

To further our understanding of how phenological progressions are structured and to predict how they may respond to climate change, we collected data from an assemblage of ten co-occurring Himalayan *Rhododendron* species on Mt. Yulong, China, through two years of phenology monitoring in transects spanning a 1400 m elevation gradient, greenhouse experiments, and in comparison with the results of long-term models of species phenological responses to temperature derived from herbarium specimens. We asked whether we could quantitatively support flowering as a multi-dimensional progression in Mt. Yulong *Rhododendron* species, whether species that are part of this progression show differential phenological responses to changes in temperature, and how these responses impact reproductive success.

We found evidence for a progression of flowering, with *Rhododendron* species significantly overdispersed in elevation and flowering time and showing significantly less inter-species overlap in flowering time-space niche (2.9%) than expected by chance (8.5%). As a whole, the progression responded to changes in weather (−2.4 days / °C) and to experimentally increased greenhouse temperatures (−9.3 days / °C). However, individual species responses varied in their response (from −26 – 2 days / °C). Models derived from historical herbarium specimens predicted contemporary observed flowering well (> 95% of plants flowering within prediction intervals) and showed corresponding species differences. Reproductive output was affected by phenology, with the quantities of flowers and fruits greater in plants which flowered slightly earlier than their population mean (flowers $p < 0.05$; fruits $p < 0.01$), and in plants that responded to warmer weather with commensurately earlier flowering (flowers $p < 0.01$; fruits $p < 0.001$).

The elaborately sequenced progression of flowering over season and elevation in Himalayan *Rhododendron* highlights the intricacy of species assemblages in time and space. Varying phenological responses among species and the associated reproductive impacts make this progression, like other staggered phenological sequences, vulnerable to disruption with ongoing climate change.

1. Introduction

Phenology is a critical dimension of natural history. The timing of key life history stages determines much about the environments to which they are exposed. In plants, reproductive phenology is particularly important, affecting gene flow, population persistence, and species boundaries (Antonovics, 2006; Kameyama and Kudo, 2009; Devaux and Lande, 2009; Ladinig et al., 2013). The staggered sequence of flowering and fruiting among species assemblages has long been a topic of interest (Clarke, 1893; Robertson, 1895). The community implications of such phenological progressions may include resource partitioning and the continuous provisioning of pollinators (Stiles, 1977; Waser and Real, 1979; Kochmer and Handel, 1986; Sherry et al., 2007) and dispersers (Wheelwright, 1985; González-Castro et al., 2012). In species assemblages that span elevational gradients, staggered flowering phenologies may be seen as multi-dimensional progressions across seasonal time

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and elevational space. However, phenological observations explicitly integrating elevational gradients remain limited to a few sites (Inouye, 2008; Wolkovich et al., 2012; Cornelius et al., 2013), despite the salience of phenology to alpine environments where late spring and early fall bracket a short period for growth and reproduction (Levesque et al., 1997; Körner, 2003).

Phenology is one of the earliest and most noticeable traits by which organisms respond to climate change (Parmesan and Yohe, 2003; Bertin, 2009; Wolkovich et al., 2014). Across the globe, reproductive phenologies have advanced with warming temperatures (Cleland et al., 2007; Wolkovich et al., 2012; Ellwood et al., 2013). However, certain species may not have sufficient plasticity or rate of adaptation to keep pace with changing climate (Visser et al., 2010; Cook et al., 2012), which may lead to species declines (Willis et al., 2008, 2010). Further, the amount and direction of phenological response may vary among species, depending on phylogenetic history (Levin, 2006; Lessard-Therrien et al., 2014) or other plant traits (Polgar and Primack, 2013; Ellwood et al., 2013). Mechanistically, different species respond to different physiological cues, including growing season temperatures, chilling requirements (Schwartz and Hanes, 2010; Cook et al., 2012), photoperiod (Amasino, 2010; Keller and Körner, 2014) and snowmelt (Inouye and McGuire, 1991; Price and Waser, 2008). These differential responses may lead to the disruption of plant flowering progressions, much as they threaten mismatches among plants and animal pollinators, seed dispersers or herbivores (Parmesan, 2006, Post et al., 2008, Forrest et al., 2010).

Seasonal gradients also may affect phenological responses to climate change, with differing responses in spring and fall phenologies or in components of phenology such as the beginning and ending of life-history events (Sherry et al., 2007; Fridley, 2012; Hart et al., 2016). These contrasts are only visible in studies that prioritize whole-season measures of phenology rather than relying solely on first flowering date (Miller-Rushing et al., 2008; CaraDonna et al., 2014). They remain less explored in phenological research (Polgar and Primack, 2013; Laube et al., 2014).

To further our understanding of how phenological progressions are structured and to predict how they may respond to climate change, we collected data from an assemblage of *Rhododendron* species on Mt. Yulong, China, near the center of distribution for *Rhododendron*. On Mt. Yulong, as elsewhere in the eastern Himalaya, *Rhododendron* species flower across broad ranges of elevation and season, are ecologically and ethnobotanically salient, and are well represented in historical herbarium collections (Hart et al., 2014; Hart and Salick, 2017; Hart and Ranjitkar, 2018). With two years of phenology data gathered across transects spanning a 1400 m elevation gradient, experimental warming treatments in high-altitude greenhouses, and comparison with the results of long-term models of phenological responses to temperature derived from these herbarium specimens (Hart et al., 2014), we asked whether we could quantitatively support flowering as a multi-dimensional progression in Mt. Yulong *Rhododendron* species, whether species or phenological components that are part of this progression show differential phenological responses to temperature, and how these responses impact reproductive success.

2. Materials and methods

2.1. Study site

At the far eastern edge of the Himalaya, Mt. Yulong (玉龙雪山 27.0 °N, 100.1 °E) occupies a geographcal nexus of the tropical lowlands of SE Asia, the subtropical and temperate vegetation of China, and the alpine Tibetan Plateau (Fig. 1A). It is the southernmost glaciated mountain in Eurasia and is located within the 'Mountains of Southwest China', a global hotspot of biological diversity (Mittermeier et al., 2005). This area is among the world's richest in temperate plant species (Kier et al., 2005) and is the center of diversity for many plant genera (Wen et al., 2014) including *Rhododendron* (Fig. 1A). More than 30% of the world's *Rhododendron* species occur in the area and half of them are endemic (Wu et al., 2005), with species richness further concentrated in northwest Yunnan and adjoining areas (Shrestha et al. 2017). Mt. Yulong (Fig. 1B, C) and the other ranges in this area (collectively called the Hengduan Mountains) are separated by deep gorges carved by the Yangtze, Mekong, and Salween Rivers. The resulting biogeographic isolation creates the high beta-diversity (Salick et al., 2004; Wen et al., 2014) that is an important component of the area's species richness. Mt. Yulong was a center of collection for the plant-hunters George Forrest and Joseph Rock (Mueggler, 2011), whose collections, along with those of later botanists, provide an exceptionally strong and well documented historical context (Hart et al., 2014).

Elevation structures vegetation communities on Mt. Yulong (Fig. 2). Above the highest agricultural fields, lower elevations (~2700 – 3300 m asl) consist mostly of pine-oak forest. With increasing elevation, vegetation grades to oak scrub (~3300 – 3700 m asl), alpine meadows (~3700 – 4100 m asl), and finally rock cliffs and retreating glaciers (Wang et al., 2007; Kong et al., 2009). At all elevations, *Rhododendron* species make up a substantial portion of the plant communities. *Rhododendron* life-forms vary depending on elevation and species: shrub understory in forest, small-tree canopy at middle and higher elevations, and dwarf shrub patches in open alpine areas and on rock outcrops.

2.2. Transect structure

We sampled *Rhododendron* populations along the elevational gradient in a stratified random pattern. We laid two transects on the eastern slopes of the mountain and two transects on the western slopes from the lowest elevation forests at the edge of cultivated land (2760 m asl on the east and 3060 m asl on the west) to the local elevational limit of *Rhododendron* species (4060 m asl). At every 100 m of elevation along each of the four transects, we set two transect points, one directly north and one directly south. Each transect point was offset a random distance between 5 and 20 m from the ascents. This produced 60 transect points on the east slopes and 44 transect points on the west slopes (Fig. 1C), at 15 elevations. From each transect point and for each *Rhododendron* species present (Table 1), we calculated plant density (as described below), monitored phenology, and recorded fruit-set. Below, we refer to the collective individuals of one species monitored around one transect point as a 'population'.

To calculate density, we used the variable area transect method (Parker, 1979), a powerful and efficient plotless density estimator which performs well with spatially aggregated distributions (Engeman et al., 1994) such as *Rhododendron* populations. From each transect point, we continued directly north or south (approximately along the elevational contour), demarking a 1.5 m wide subtransect of variable length. For the first four plants of each *Rhododendron* species encountered, we measured: distance along the subtransect, height and maximum horizontal canopy cover. The density of a given species (plants / m^2), was calculated as $D = (nr - 1) / (w\ \Sigma\ l_i)$, where n is the number of subtransects, r is the nth plant (here, 4), w is the search width (here, 1.5 m), and Σl_i is the sum of lengths (distances from the transect point) to the rth (4th) plant. If 50 m along the subtransect was searched encountering 1–3 plants of a species, the species was recorded as low density (which we quantified as $D = 0.005$ for the purposes of aggregation), and if no plants were encountered, the species was recorded as absent. Species were identified in the field according to the local plant checklist (Wang et al., 2007). We collected voucher specimens of each species to confirm identification with reference to the Flora of China (Wu et al., 2005) and deposited specimens at the herbaria of the Kunming Institute of Botany-Chinese Academy of Sciences (KUN) and the Missouri Botanical Garden (MO).

For phenological monitoring of *Rhododendrons* at each point, we tagged the nearest 12 plants of each species present for repeat monitoring. For the entire flowering period (February to August) in 2012

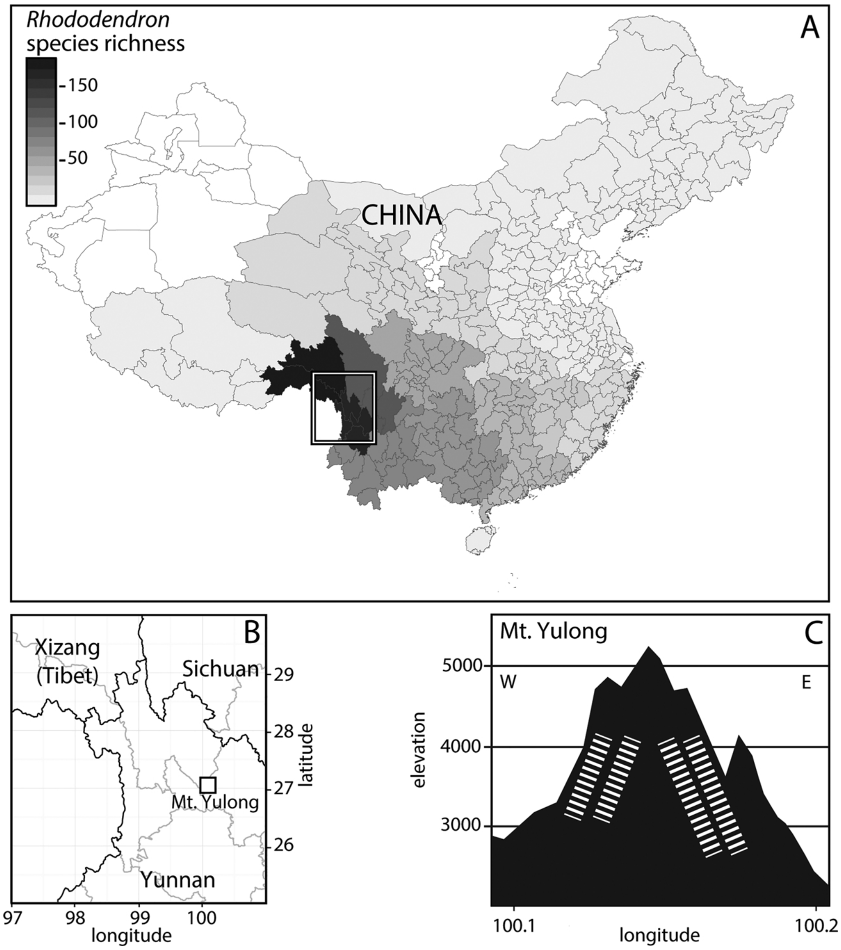

Fig. 1. Transects on Mt. Yulong sample a hotspot of Rhododendron species richness. A) *Rhododendron* species richness is concentrated in Southwest China, particularly in the Hengduan Mountains, where northwest Yunnan meets southeast Tibet and southwest Sichuan (compiled from species location data in *Flora of China* (Wu et al., 2005). B) Mt. Yulong is located in Northwest Yunnan at the center of this hotspot of *Rhododendron* species richness. C) Two transects each were constructed on east and west aspects of Mt. Yulong from the lowest elevation forests at the edge of cultivated land (2760 m asl on the east and 3060 m asl on the west) to the local elevational limit of *Rhododendron* species (4060 m asl).

and 2013, we recorded the phenological state of each plant twice monthly (13–17 day intervals). We quantified phenological state by counting the number of inflorescences on each plant bearing flower buds showing color (hereafter, ‘budding’), the number of inflorescences bearing flowers in anthesis (‘flowering’) and the number of inflorescences bearing flowers past anthesis (‘past’). As a measure of reproductive success in 2013 we recorded the number of inflorescences bearing mature fruits (‘fruiting’).

For each plant, we computed a single value for mean flowering day as the mean of observation dates weighted by number of flowering inflorescences $\Sigma\ o_i\ (f_i\ /\ \Sigma\ f_i)$, where o_i is the day number of each observation, f_i is the number of inflorescences observed on that day for an individual plant i and $f_i / \Sigma f_i$ is the normalized number of inflorescences. Very infrequently, all flowering had taken place between observation dates. In these cases, where we observed past inflorescences without previously recorded flowering inflorescences, we assigned mean flowering day as the midpoint between the date when past flowers were observed and the previous observation date.

2.3. Flowering across elevation and season

To test for the effects of elevation on phenology, we constructed linear regressions of plant mean flowering day with elevation within each species and across the genus.

To test for overdispersion of flowering among species, we constructed a Poisson family generalized linear model (glm) of the number of species flowering as a response to elevation and month, and tested for a significant difference from equidispersion. To further test whether this overdispersion of flowering could be related to limiting similarity, we measured niche overlap following the methods of Albrecht and Gotelli (2001). In this analysis, we categorized species by season as early-season (mean flowering before Julian day 130), mid-season (between days 130 and 160) and late-season (after day 160). In each combination of the 14 elevations and three seasons, we calculated a Czechanowski overlap index (Feinsinger et al., 1981) for each pair of species as $1 - 0.5\ \Sigma\ (p1_i - p2_i)$, where $p1_i$ and $p2_i$ are the proportions of populations of species 1 and 2, respectively, with their mean flowering at an elevation-season combination i. We then used a permutation test to assess significance on the basis of 1000 randomizations in which records were reassigned within species across elevation-season combinations (Albrecht and Gotelli, 2001).

To examine how elevation affects variability, we used linear regression to model response to elevation of the standard deviation of mean flowering day within populations and among species at the same elevations. Individual variance was calculated as the deviation of the mean flowering day of an individual from the population mean flowering day $f_i - \Sigma\ (f)\ /\ 12$ where f_i is the mean flowering day of the individual and $\Sigma\ (f)\ /\ 12$ is the mean flowering day for the 12 plants within the population.

2.4. Phenology and temperature

We compared observed flowering times against our model for temperature effects on *Rhododendron* phenology (Hart et al., 2014). In this generic model, derived from herbarium specimens collected between 1885–2009, mean flowering day responds to a ‘warming effect’ (2.26 days earlier / °C deviation in preceding-year mean annual temperature), a ‘chilling effect’ (2.54 days later / °C deviation in preceding-year mean fall temperature), and elevation (1.4 days later / 100 m deviation in elevation from the species mean). We applied the model to

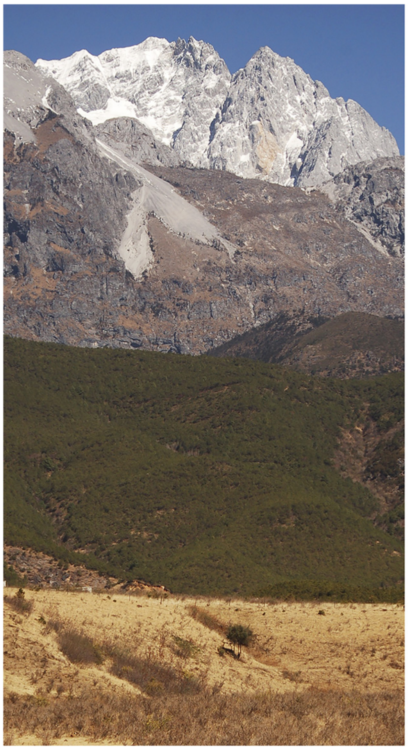

Fig. 2. Elevation structures vegetation communities on Mt. Yulong. High agricultural fields border a gradient from pine-oak forest to oak scrub, alpine meadows and limestone outcroppings and glaciers. Pictured here are the eastern slopes, which range from the Lijiang Basin (2600 m asl) in the foreground to the receding Yanggong Glacier (~5000 m asl) and Satseto Peak (5596 m asl) in the background.

weather data from the Lijiang weather station of the China Meteorological Administration to predict mean flowering day on Mt. Yulong. Hart et al. (2014) also report specific models of mean flowering day for nine of the ten species monitored here. For the genus and for each of these species we compared the model predictions for mean flowering day in 2012 and 2013 with the observed mean flowering day in those years. As a measure of fit, we calculated the percentage of plants whose mean flowering day was within the 95% prediction interval of the models.

As a measurement of plant phenological response to temperature, we calculated variation between the years as the difference between the mean flowering day of an individual plant (f_i) in 2012 and in 2013 ($R = f_{i2013} - f_{i2012}$). This interannual difference was taken as a measurement of temperature sensitivity. We used a paired Wilcoxon analysis to test for significant differences in mean flowering day of individuals in 2012 and 2013. We also tested if the amount of temperature sensitivity responded to elevation by constructing a hierarchical linear mixed model of temperature sensitivity over elevation, blocked within species.

Our previous work (Hart et al., 2016) has shown last flowering day (but not first or mean flowering day) to be related to shared evolutionary history within the genus *Rhododendron.* To further test whether first or last flowering day might constrain phenological response to temperature, we also calculated interannual difference in first and last flowering day, and used Wilcoxon tests to examine whether these differences were significantly positive or negative.

To experimentally test phenological response to temperature, we transplanted rhododendrons into a greenhouse at the field station. We chose the two common species growing at the same elevation as the greenhouse (3260 m asl), *R. racemosum* and *R. hippophaeoides*, and transplanted 30 individuals of each species from one population into the greenhouse in August 2011. We marked 30 randomly chosen individuals of each species that remained in the source population as field controls and monitored both the greenhouse and field species phenology with the same methods employed along the transects. Temperature measurements taken in the field populations and greenhouse throughout the year indicated that temperatures were an average 3.5 °C higher in the greenhouse. Because of low rates of flowering, particularly for *R. hippophaeoides*, in both the field population and greenhouse, we transplanted an additional 15 *R. racemosum* and 30 *R. hippophaeoides* in September 2012 and marked equal numbers of individuals for monitoring in the control population. Because mean flowering date was similar in both years, we include both years of data in the results below. We calculated mean flowering day as in the elevational transect observations and tested for significant differences between controls and greenhouse treatments with linear mixed effects models, blocked by year.

2.5. Reproductive effects

To explore the reproductive effects of phenological deviation, we constructed Poisson glms of two reproductive measures: (1) fruiting inflorescences, as measured in 2013, and (2) total inflorescences, which measured the number of flowering inflorescences that had completed anthesis, and was calculated as the maximum (final) count of past inflorescences. These measures of reproductive success were compared to the phenological deviation of each individual mean flowering day from the population mean flowering day ($f_i - \Sigma (f) / 12$). To test the effects of temperature sensitivity on reproduction, we constructed similar Poisson glms to explain total inflorescences and total fruits with temperature sensitivity as an independent variable. In these analyses, we modeled both phenological deviation and temperature sensitivity as linear and quadratic terms to account for potential effects of earlier and later variance.

Linear and glm modeling and permutation analyses used the base package of the statistical framework R 3.1.1 (Venables and Ripley, 2002) and dispersion testing used the R package AER (Kleiber and Zeileis, 2008).

3. Results

3.1. Flowering across elevation and season

At 104 transect points from which we monitored *Rhododendron* phenology, we measured in each year (2012 and 2013) 113 populations and 1356 individual plants (Table 1). Ten *Rhododendron* species were encountered in the subtransects (Fig. 3), and the number of *Rhododendron* species co-occurring around a single transect point ranged from 0 to 4. The number of co-occurring species increased with elevation ($y = 0.0007x - 0.6959$, $p = 0.006$, $r^2 = 0.09$). Simple linear regression showed a significant relationship of later flowering (increasing Julian day) at higher elevations across the genus (2012: $y = 0.055x - 53.87$, $p < 0.001$, $r^2 = 0.36$; 2013: $y = 0.044x - 17.99$, $p < 0.001$, $r^2 = 0.33$) and for most species in both years (Fig. 4). No significant relationship in either year was found in *R. adenogynum* and *R. primuliflorum*, which were only encountered at two elevations, or in *R. yunnanense* which was encountered at four elevations (Table 1, Table S1).

Rhododendron species and flowering were widely distributed across elevation and season (Table 1). Mean flowering among *Rhododendron* populations ranged from February to August (Julian days 88–218) and the elevations at which species had their highest densities ranged from 3360 to 3960 m asl. A fitted Poisson glm for number of species flowering by elevation, month and their interaction ($y = -1.543x - 0.002z + 0.0004xz$) was significantly overdispersed ($alpha = 0.37$, $p = 0.01$), confirming greater spread among species in elevation and season than expected by chance. Thus, each seasonal cohort had low, mid and high elevation species (Fig. 5). The observed overlap among flowering niches defined by elevation and season was only 2.9%, significantly lower than

Table 1
Summary metrics of *Rhododendron* sp. by elevation and species: density (plants/m^2); number of plants monitored (each population consists of 12 plants), and for 2012 and 2013: percentage of plants flowering and the mean and standard deviation of mean flowering day of individuals.

elevation (m asl)	density (plants/m^2)	N (# individuals)	plants flowering in 2012 (%)	flowering day in 2012 ($\bar{x}$ ± sd)	plants flowering in 2013 (%)	flowering day in 2013 ($\bar{x}$ ± sd)
R. racemosum						
2760	0.29	48	44	88 ± 7	15	90 ± 8
2860	0.03	48	42	93 ± 8	42	124 ± 15
2960	0.34	24	46	93 ± 7	21	86 ± 7
3060	0.12	48	56	91 ± 9	42	98 ± 28
3160	0.005	48	48	115 ± 34	65	109 ± 28
3260	0.10	72	42	113 ± 8	63	134 ± 14
3360	0.82	48	92	118 ± 4	85	112 ± 5
3460	0.005	36	72	134 ± 7	44	130 9 ±
R. rubiginosum						
3160	0.005	48	52	107 ± 7	50	111 ± 10
3260	0.005	48	25	103 ± 6	58	113 ± 15
3360	0.005	24	58	118 ± 6	75	113 ± 8
3460	0.04	60	50	131 ± 7	55	134 ± 11
3560	0.48	72	63	130 ± 5	83	124 ± 7
3660	0.25	36	28	137 ± 9	75	138 ± 11
R. beesianum						
3760	0.04	24	79	127 ± 6	75	115 ± 6
3860	0.005	24	63	132 ± 4	75	136 ± 6
R. yunnanense						
3060	0.005	24	71	132 ± 5	38	139 ± 8
3160	0.005	24	63	158 ± 19	42	150 ± 6
3260	0.04	24	71	142 ± 6	79	144 ± 6
3360	0.34	24	75	142 ± 8	88	145 ± 7
R. oreotrephes						
3460	0.50	48	77	151 ± 8	58	146 ± 5
3560	0.38	24	67	154 ± 7	50	147 ± 5
3660	0.03	36	33	151 ± 7	47	155 ± 5
3760	0.005	12	100	148 ± 3	100	152 ± 4
R. traillianum						
3560	0.005	12	75	129 ± 2	58	130 ± 3
3660	0.005	36	75	138 ± 4	83	133 ± 5
3760	0.05	24	67	141 ± 3	75	143 ± 4
3860	0.005	24	25	142 ± 3	79	148 ± 2
4060	0.005	12	58	151 ± 4	92	150 ± 2
R. adenogynum						
3960	0.27	36	81	158 ± 6	86	156 ± 5
4060	0.01	36	75	161 ± 5	75	160 ± 6
R. lepidotum						
3160	0.52	24	100	209 ± 7	67	184 ± 6
3460	0.89	24	63	218 ± 3	42	197 ± 7
R. impeditum						
3560	0.005	12	92	144 ± 11	92	153 ± 7
3660	0.37	36	97	167 ± 25	92	156 ± 9
3760	0.005	12	100	165 ± 9	83	158 ± 8
3860	0.23	36	92	165 ± 12	100	163 ± 8
3960	0.13	24	88	171 ± 10	75	167 ± 7
R. primuliflorum						
3960	0.81	36	92	165 ± 7	92	167 ± 7
4060	0.01	36	98	165 ± 7	85	168 ± 8

expected (8.5%, confidence interval 5.8%–11.7%) (Fig. 6). These patterns create an elaborate phenological progression over time and elevation.

Three measures of synchrony in flowering increased with elevation. First, intraspecies flowering times were compressed, i.e. higher elevations were significantly associated with smaller standard deviations of mean flowering day within populations ($y = -0.002x + 13.7$, $p = 0.013$, $r^2 = 0.03$) (Fig. 7A). Second, interspecies flowering times were compressed, i.e. standard deviation among populations of different species around the same monitoring point also decreased with elevation ($y = -0.029x + 122.4$, $p < 0.001$, $r^2 = 0.43$) (Fig. 7B). Third, the absolute value of individual deviation from the population mean decreased with elevation (linear mixed effects model across-species fit values 2012: $y = -0.004x + 18.92$, $p = 0.001$; 2013: $y = -0.004x + 21.47$, $p < 0.001$).

3.2. Phenology and temperature

In both 2012 and 2013, observed phenology was comparable to that predicted from the herbarium-derived model. Lijiang weather station data showed preceding-year mean annual temperature (to account for overall warming) and preceding-year mean fall temperature (to account for chilling) respectively for 2012 to be 13.04 °C and 15.90 °C, and for 2013 to be 13.81 °C and 16.04 °C. As deviations from the long-term mean, these are + 2.43 °C and + 2.51 °C in 2012 and + 3.20 °C and + 2.64 °C in 2013. Using these temperature deviations, mean flowering day was predicted for each elevation with the generic model, and for each species model (Table 2, Fig. S1). In both years, nearly all

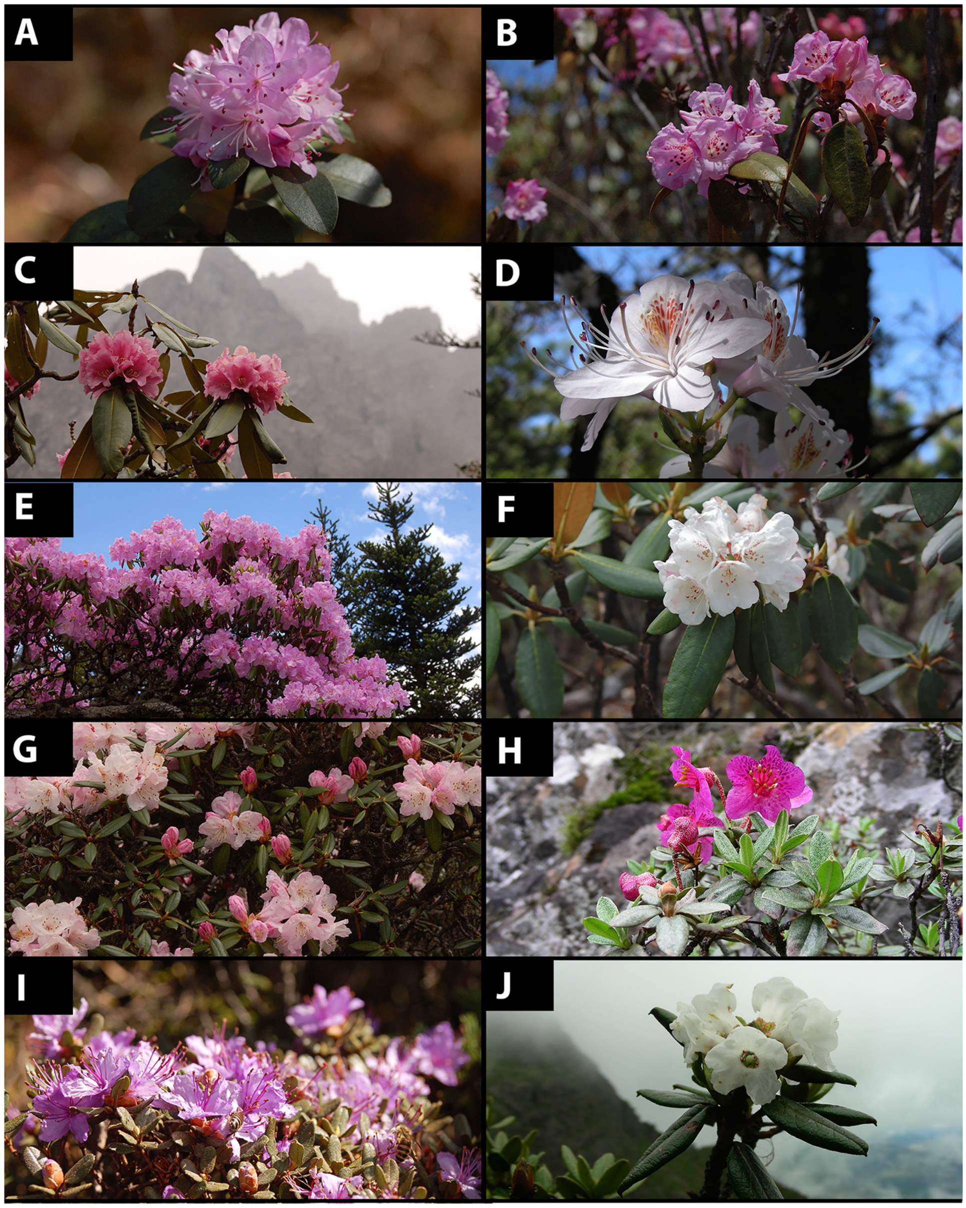

Fig. 3. Ten *Rhododendron* species flowering on Mt. Yulong were monitored along gradients of season and elevation: A) *R. racemosum* Franch., B) *R. rubiginosum* Franch., C) *R. beesianum* Diels, D) *R. yunnanense* Franch., E) *R. oreotrephes* W.W. Sm., F) *R. traillianum* Forrest & W.W. Sm., G) *R. adenogynum* Diels, H) *R. lepidotum* Wall. Ex G. Don, I) *R. impeditum* Balf. f. & W.W. Sm., J) *R. primuliflorum* Bureau & Franch.

plants observed had a mean flowering day within the 95% model prediction intervals (99% of plants within the prediction intervals in 2012 and 96% in 2013). Within these margins, plants tended to flower slightly earlier than predicted from the herbarium-derived model: in 2012 the mean observed generic flowering time was 6 days earlier than the predicted flowering time and in 2013 it was 8 days earlier. This trend across the genus was also evidenced for most species (Table 2), with *R. yunnanense* a notable exception.

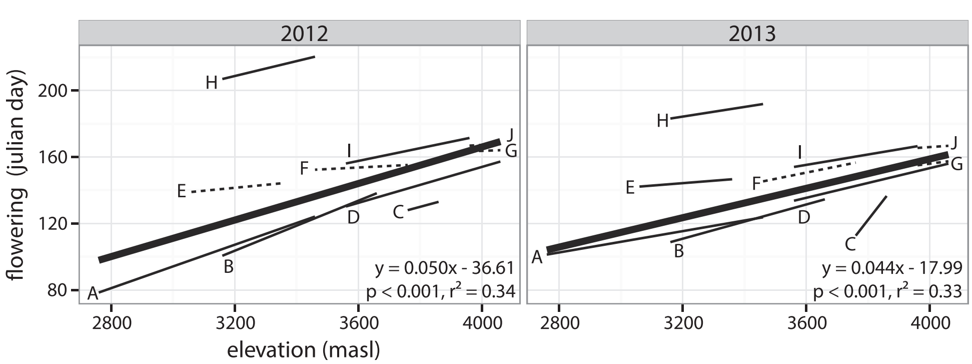

Fig. 4. Time of *Rhododendron* flowering is later at higher elevations. Linear regressions for all *Rhododendron* species combined (bold lines) show significantly later mean flowering day at higher elevations. Separate regressions for most species (regression lines with letters coding species as in Fig. 3) show a similarly later mean flowering day at higher elevations (nonsignificant species regressions shown as dotted lines, full regression equations for all spp. in Table S1).

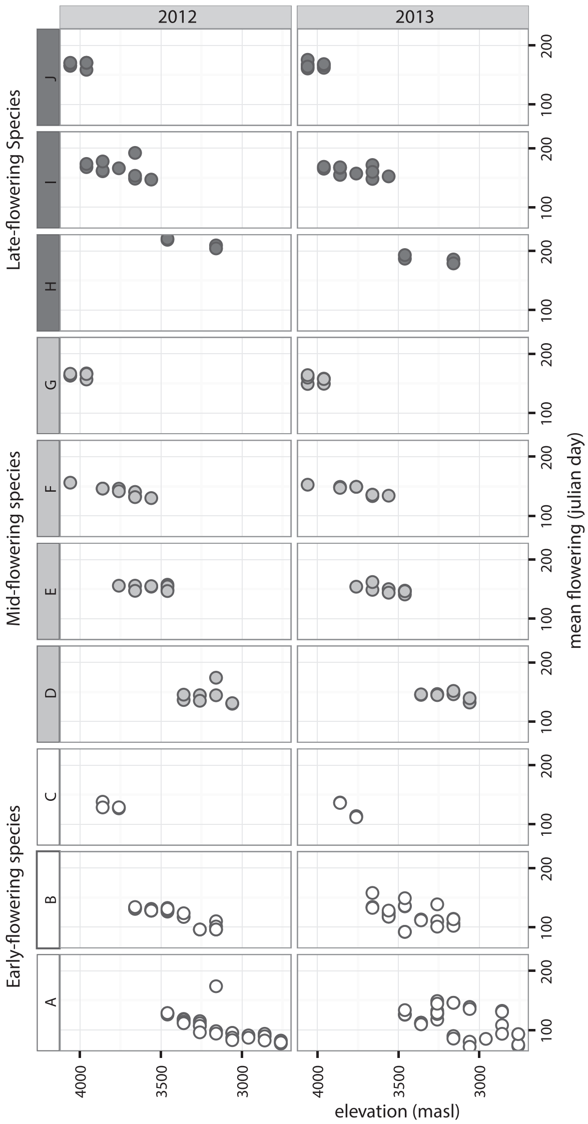

Fig. 5. Phenological progression over season and elevation. In both 2012 and 2013, flowering of *Rhododendron* species at a given season are dispersed over elevation, and species within an elevational band flower sequentially. Each pane contains populations of one *Rhododendron* species with letters coding species as in Fig. 3. Shades indicate seasonal cohorts based on species mean flowering time: white: early-season (before Julian day 130), light grey: mid-season (between day 130 and 160), and dark grey: late-season (after day 160).

Among individual plants that flowered in both years, mean flowering day in 2013 was significantly earlier (Wilcoxon paired analysis $p < 0.001$) by 2.36 ± 0.91 days, while annual temperatures increased by 0.77 °C. This response to temperature decreased with elevation: the phenological response to annual temperature change was significantly less at higher elevations (linear mixed effects model fit values $y = -0.007x + 33.98$, $p = 0.001$). Within species, flowering was also significantly earlier in 2013 (Wilcoxon paired $p < 0.05$) for *R. beesianum* (−8.1 days), *R. oreotrephes* (−3.4 days), *R. adenogynum* (−8.0 days), and *R. lepidotum* (−26 days). Only *R. yunnanense* flowered significantly later in 2013 (by +2.0 days).

Considering other phenological components, the first flowering day of individual plants, similarly to mean flowering day, was significantly earlier in 2013 (4 days earlier, Wilcoxon 95% confidence interval 3–4.5, $p < 0.001$). In contrast, last flowering day did not show a significant change (Wilcoxon 95% confidence interval −1.5 – +3, $p = 0.48$).

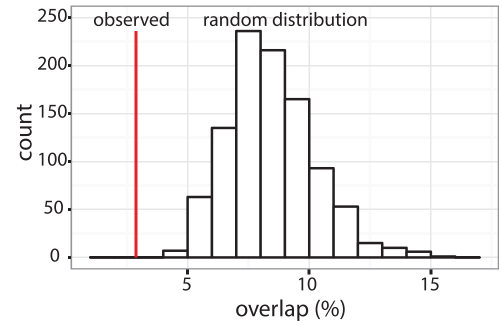

Fig. 6. *Rhododendron* niche overlap was significantly less than expected by chance. The mean overlap between elevation-season flowering niche (the proportion of populations of a species flowering in each combination of the 14 elevations and three seasons) for all observed species pairs was only 2.9% (vertical line). This is significantly lower than the distribution of overlaps for 1000 simulated randomized populations (histogram, mean 8.5%, confidence interval 5.8–11.7%).

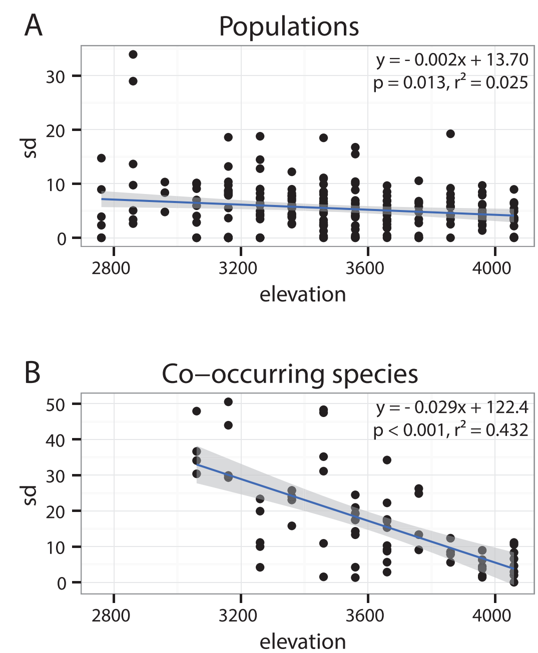

Fig. 7. Flowering synchrony is greater at higher elevations. Standard deviations (sd) of mean flowering day decreased with elevation both within and among species. A) Within populations of a species, mean flowering day sd decreased with increasing elevation ($y = -0.002x + 13.7$, $p = 0.013$, $r^2 = 0.03$). B) At sites with more than one species, mean flowering day sd among species significantly decreased with increasing elevation ($y = -0.029x + 122.4$, $p < 0.001$, $r^2 = 0.43$).

In both 2012 and 2013, individuals transplanted into the greenhouse flowered much earlier than the field population (Table 3). Linear mixed effects model results blocked within year were, for *R. racemosum*, $y = -39x + 122$, $p < 0.001$, and for *R. hippophaeoides* $y = -31x + 135$, $p < 0.001$. The effect was dramatic enough that there was almost no overlap in flowering between the control and greenhouse populations (Fig. 8).

3.3. Reproductive effects

The number of flowering inflorescences and fruiting inflorescences was greater in plants with individual mean flowering day slightly earlier than mean flowering day of their population, and in plants that flowered slightly earlier in 2013 than 2012 (tracking warming). Poisson glms showed reproductive output to respond significantly both to the

Table 2
Modeled and observed phenologies are comparable. Predicted mean flowering day is derived from the generic and specific models derived from herbarium specimens (Hart et al., 2014), parameterized with preceding-year annual and fall temperatures. The mean of the predictions made for each elevation (Fig. S1) is similar to mean flowering observed in the transects. The percentage of plants with an observed mean flowering day within the 95% prediction intervals of the herbarium-derived model (% fit) is close to 100% with the exception of *R. beesianum* in 2013.

Rhododendron species	Predicted species mean flowering day 2012	Observed species mean flowering day 2012	% fit 2012	Predicted species mean flowering day 2013	Observed species mean flowering day 2013	% fit 2013
Genus	156	150	96%	154	146	99%
R. racemosum	129	102	95%	127	110	93%
R. rubiginosum	148	118	100%	142	120	100%
R. beesianum	155	131	100%	154	125	50%
R. yunnanense	140	143	100%	138	144	100%
R. oreotrephes	164	153	100%	163	150	100%
R. adenogynum	174	164	100%	168	156	100%
R. lepidotum	195	213	100%	195	186	100%
R. impeditum	168	163	99%	162	160	100%
R. primuliflorum	181	167	100%	181	166	100%

Table 3
Phenology advances with artificially elevated temperatures. Compared to individuals in the source population from which they derived, individuals of *R. racemosum* and *R. hippophaeoides* transplanted into a high-elevation greenhouse (at a mean of 3.5 °C > outside temperatures) had a mean flowering day 28–30 days earlier in 2012 and 30–45 days earlier in 2013. Additional individuals were added to both the control and greenhouse groups for the 2013 monitoring because of low flowering rates (17%–83%) in the first year.

	2012N plants flowering / total	2012 mean flowering day ± sd	2013N plants flowering / total	2013 mean flowering day ± sd
R. racemosum				
Control	21 / 30	123 ± 9	25 / 45	122 ± 9
Greenhouse	25 / 30	93 ± 14	36 / 45	77 ± 15
R. hippophaeoides				
Control	16 / 30	135 ± 6	23 / 60	135 ± 8
Greenhouse	5 / 30	107 ± 11	27 / 60	105 ± 14

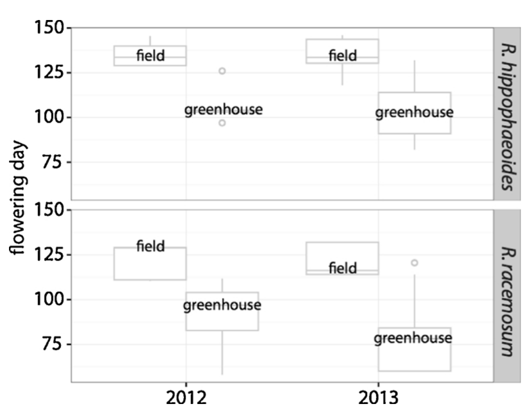

Fig. 8. Advance in flowering phenology with warming is dramatic enough that there is almost no overlap between field and greenhouse populations. In both 2012 and 2013, individuals of *R. racemosum* and *R. hippophaeoides* transplanted into a + 3.5 °C greenhouse flowered much earlier than those of the field population. Linear mixed effects model results blocked within year were, for *R. racemosum*, $y = -39x + 122$, $p < 0.001$, and for *R. hippophaeoides* $y = -31x + 135$, $p < 0.001$.

deviation of a plant from the mean of the population and to phenological differences between years. Later mean flowering day, as well as large deviations from the population mean flowering day in either direction, reduced quantity of both flowering inflorescences ($y = -0.032x - 0.001x^2 - 0.071$, $p = 0.02$; Fig. 9A) and fruiting inflorescences ($y = -0.041x - 0.002x^2 - 0.327$, $p = 0.005$; Fig. 9B). Similarly, later mean flowering day of a plant in 2013 (the warmer year) than in 2012, as well as greater difference between years in either direction, reduced quantity of both flowering inflorescences ($y = -0.022x - 0.001x^2 - 0.055$, $p = 0.009$; Fig. 9C) and fruiting inflorescences ($y = -0.029x - 0.001x^2 - 0.136$, $p < 0.001$; Fig. 9D).

4. Discussion

4.1. Flowering across elevation and season

The changing bands of flower color over season and elevation that suggest phenological progressions in the eastern Himlaya have been noted in the past. Victorian plant hunter Frank Kingdon-Ward wrote eloquently of the *Rhododendron* species that cover these mountains in “a tidal wave of tense colours which gleam and glow in leagues [and] leap at you as you climb” (Kingdon-Ward, 1926). This impressive display inspired Kingdon-Ward, Joseph Rock, George Forest, and successive generations of collectors (Wagner, 1992; Mueggler, 2005; Glover et al., 2011; Mueggler, 2011) to collect the super-numerous specimens that make comparative studies today possible (Hart et al., 2014). The same salience also inspires the local Yi and Naxi peoples to attribute spiritual importance and practical agricultural timing to *Rhododendron* flowering phenology (Hart and Salick, 2017). Our results have provided quantitative evidence and ecological context for these past qualitative observations, showing that the progression of flowering through season and elevation (Fig. 5) may be quantitatively supported through significantly reduced overlap among species in seasonal-elevational flowering niche (Fig. 6).

Flowering progressions such as these have been suggested to reflect evolutionary and ecological pressures including temporal and spatial barriers to hybridization (Antonovics, 2006; Levin, 2006; Devaux and Lande, 2009) and/or the partitioning of flowering across time as a resource (i.e., competition for pollination service; Waser and Real, 1979; Kochmer and Handel, 1986; Sherry et al., 2007). Rhododendrons do hybridize in the wild (Milne et al., 2003; Ma et al., 2010) and share at least common floral visitors (especially *Apis cerana* and diverse *Bombus* species) but thorough assessments of pollinator behavior and pollinator limitation await future work (Georgian et al., 2015; Huang et al., 2017).

The greater interspecific flowering synchrony (Fig. 7) we observed at higher elevations may be evidence for the increased relative influence of abiotic versus biotic constraints at these elevations: species are limited to a narrow seasonal window of suitable temperatures. Other studies have also associated higher elevations with a reduction in relative importance of biotic pressures such as competition for pollinators (Callaway et al., 2002; Ghazoul, 2006).

4.2. Phenology and temperature

Although we observed earlier flowering with warmer temperatures

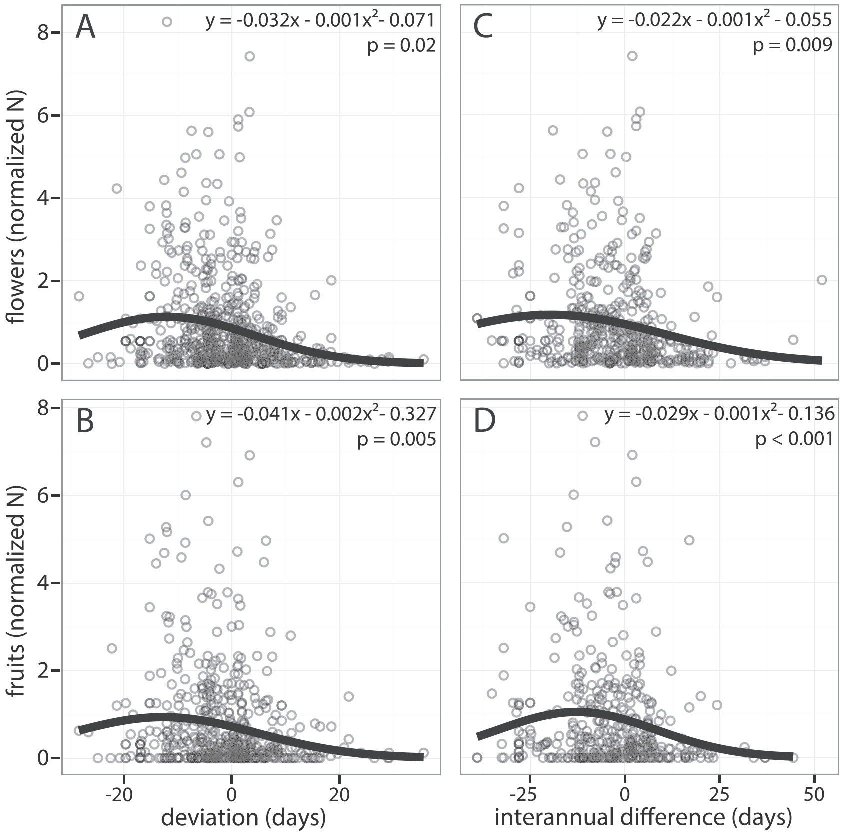

Fig. 9. Reproductive advantage of earlier flowering and fruiting. Numbers of flowers and fruits are greater in plants with mean flowering day slightly earlier than their population mean flowering, and in plants that flowered slightly earlier in 2013 than 2012. Poisson glms (blue line) show that plants with positive deviation (mean flowering day later than the population mean) and plants with large deviation in either direction evidence A) reduced quantity of flowering inflorescences (normalized by species) and B) reduced quantity of fruiting inflorescences (normalized by species). Plants with positive interannual difference (later mean flowering day of a plant in 2013 than 2012) and plants with large interannual difference in either direction showed C) reduced quantity of flowering inflorescences and D) reduced fruiting inflorescences (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(a) across *Rhododendron* as a genus with warmer temperatures in 2013, (b) with elevated temperatures experienced in the greenhouse experiments, and (c) at lower elevations, a common proxy for warmer temperatures (Nagy and Grabherr 2010), there were distinct differences in the amount of response among species and among phenological components. These differential responses may be driven by differences in phenological cues such as day length and chilling/vernalization (Amasino, 2010; Hart et al., 2014) and are reflected in phylogeny (Hart et al., 2016). The phenologies of other life history events, such as leaf-out, may also affect how species flowering phenology responds to temperature. For example, *R. yunnanense* flowered later than predicted by the specimen-derived model, later with warmer temperatures in 2013 and did not show a significant change in flowering time with elevation (Fig. 6). *R. yunnanense* is also the only fully deciduous species on Mt. Yulong, flowering before leaf-out. Intriguingly, *R. yunnanense* also flowered later with warmer temperatures in studies done at Royal Botanic Gardens Edinburgh 2002–2009 (Harper, 2010).

There is an emerging recognition that analyzing more comprehensive components of phenology — including end of phenologies within and among individuals and species — is important to understanding phenological changes (Fridley, 2012; Wolkovich and Cleland, 2014; Gallinat et al., 2015). This is borne out by our finding that last flowering day, unlike first and mean flowering day, did not show interannual change. Last flowering day of Mt. Yulong *Rhododendron* species has been associated with phylogeny and floral morphology (Hart et al., 2016), which may constrain the responsiveness of this phenological component to changing temperatures.

We observed different rates of change among our different methods, with change in phenology between years greater than predicted from the historical herbarium-derived model (Table 2). Potential causes of this increased advanced flowering are the greater power available from comprehensive ecological sampling, temporal scale effects (Wolkovich et al., 2014), and/or increased recent warming and a nonlinear response to temperature increases as climate change takes its toll (Iler et al., 2013). Likewise, if the phenological differences along the elevational gradient in our study are taken as a response to temperature differences over elevation (using an adiabatic lapse rate of 0.6 °C / 100 m; Nagy and Grabherr 2010) then the change in phenology across elevation is equivalent to 6.5–9.5 days / 1 °C, greater than either the observed or modeled responses to weather. This parallels other studies that have shown differences across elevations to exceed those expected with adiabatic lapse rate calculations (Cornelius et al., 2013). These differences may suggest local adaptation along the elevational gradient (Wang et al., 2014) or a non-linear response, because temperature differences between the highest and lowest populations exceeded those between years. The comparably high rate of phenological response we observed in the greenhouse experiments (8.5–12.9 days / °C) may support the latter explanation.

4.3. Reproductive effects

Flowering phenology may directly affect plant fitness through biotic pressures on reproduction (e.g., pollination success) as well as abiotic pressures (e.g., temperature effects on fruit development). Our results showing that plants that flowered much earlier or later had reduced reproductive output (Fig. 9A, B) may reflect normalizing selection (Devaux and Lande, 2008; Koenig et al., 2012). Similarly, reproductive output was increased in plants that responded to annual differences by flowering earlier with the warmer temperatures in 2013, but was reduced by too great a deviation from the phenological progression over season and elevation (Fig. 9C, D). The reduction in fitness could be associated with physiological pressures, as seen in studies where flowering time is experimentally modified through elevational transplanting (Scheepens and Stöcklin, 2013) or biotic forces, as when plants, and not their pollinators, respond to annual temperature changes (Cleland et al., 2007).

5. Conclusion

Especially important in predicting the effects of future climate change, studies showing direct connections between phenology and reproductive success are comparatively rare, and tend to reveal very different patterns in different ecosystems (Chuine, 2010). We observed that variations in both phenological progression and response to annual temperature directly impacted reproductive success. This indicates that moderate change in response to annual temperature variation may be beneficial. However, the varying phenological responses among species and phenological components (first vs. last flowering day) suggest the possibility that differential future phenological responses to climate change could alter the sequenced progression of *Rhododendron* flowering.

Phenological progressions over season and elevation within and across plant genera are widespread in montane and alpine environments. These are among the ecosystems most vulnerable to climate change and are experiencing some of the most rapid changes (Mountain Research Initiative EDW Working Group, 2015). While we have suggested how these progressions may be changed by shifting phenologies, they may also be reshaped by moving plant elevational ranges (Gottfried et al., 2012; Steinbauer et al., 2018). This possibility calls for synergistic research in order to predict these changes, and to understand their consequences to the functions of phenological progressions.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ppees.2018.09.001.

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